NOCTURNAL MIGRATION IN ILLINOIS— DIFFERENT POINTS OF VIEW

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Since 1957, with other colleagues of the Illinois Natural History Survey. I have attempted by various means to observe and describe night migration of birds in central Illinois. Our accumulation of data includes more than 3 years of radar observations on film. audio records on magnetic tapes. specimen data from birds killed at television towers. and field censuses of migrants in fall and spring. 1957–1963. From these records. data have been published on the methods of study (Graber and Cochran. 1959: Graber and Hassler. 1962). and on some general characteristics of migration in this region (Hassler et al.. 1963: Bellrose and Graber. 1963).

The application of a variety of techniques to the study of migration seems. at times. to confuse rather than clarify the picture. Some of our observations made using different techniques seem even to be contradictory. and yet each method of study probably contributes something to our understanding of the truth.

The objectives of the present paper are to show how different methods of study influence our perception of the truth. and to point out certain consistent traits of night migration in this region. particularly with regard to variation in the volume and direction of migration under various conditions.

METHODS

This paper is based primarily on direct observations of migration, made in central Illinois between 1960 and 1962. The radar and aural methods of study and the equipment used have already been described for the most part (Graber and Cochran. 1959: Graber and Hassler. 1962).

In 1961 I added a mobile radar unit to our equipment. This unit consisted of an APS-42A radar set and portable gasoline generator. mounted in a covered pickup truck (Fig. 1). In the fall. 1961. and spring. 1962. I ran east-west and north-south transects with the mobile unit along highways in the states of Illinois, Indiana and Iowa in order to learn whether the direction of migration varied from place to place. In running transects. the radar was usually operated for periods of 20 to 30 minutes at each stop. and the stops were spaced 20 to 40 miles apart. Because the directional scale on the mobile radar indicators was tied to the truck. accuracy of the directional data from the mobile radar depended on accurate placement of the vehicle. The truck was positioned on the basis of the north star and detailed road maps.

One interpretation which I have made of the radar record needs further

Fig. 1. Mobile radar unit used to observe bird migration at several localities in Illinois.

explanation. An observer watching the radar PPI indicator sees two basic patterns in the display of targets. Most conspicuous are targets moving tangential to the rotating radar beam. Such targets leave a track of spots glowing on the radar scope which mark the progress of the target as it moves through the sky. It is axiomatic that the recording of a track depends upon the target holding its altitude and direction relatively constant through the area covered by the radar beam sweep. Non-tangential targets are usually intercepted by the radar beam only once, if at all. For every tracking bird target observed, usually two to three non-tracking (non-tangential) targets are intercepted (see photo, Graber and Hassler, 1962:372). In working with the radar data, I noticed that the ratio of tracking to non-tracking targets varied from hour to hour, and sometimes from night to night. Feeling that this variation might be related to orientation (or lack of orientation) of migrants, I calculated the "tracking ratio" for each hour of the night for a number of nights (Sept. 1–2, 4–5, 9–10, 11–12, and 13–14, 1960), and found that on clear nights the ratio varied from hour to hour in a consistent pattern. The significance of this pattern and observed deviations from it are discussed below.

To show how widespread are the tracks of the migrant swarm which passes in view of the Champaign radar on a given night, I have extrapolated

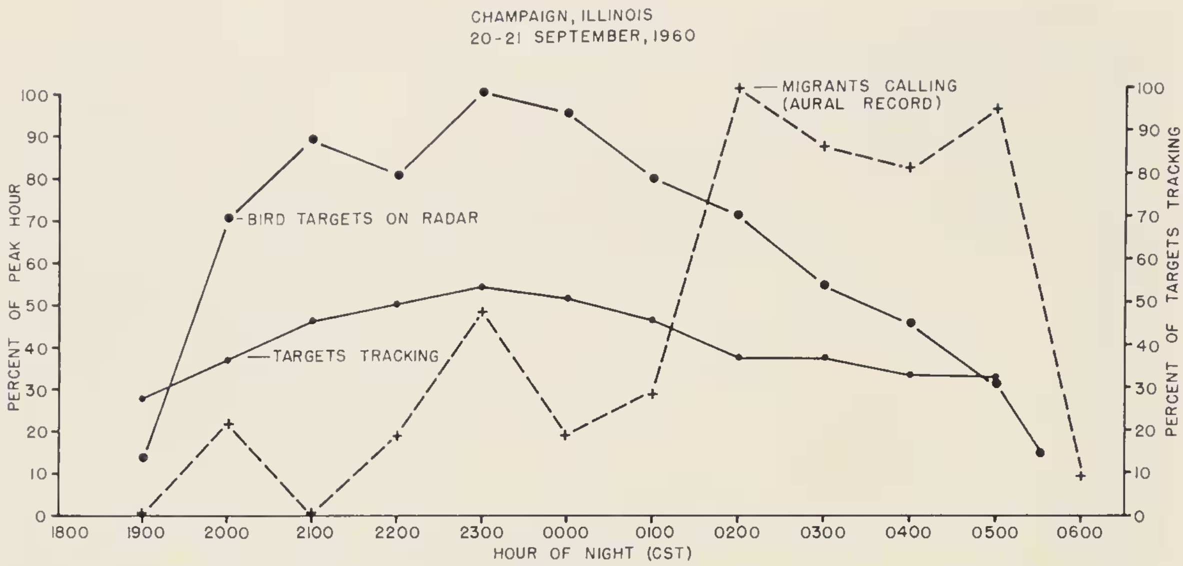

FIG. 2. Comparison of temporal patterns of migration as recorded simultaneously by radar and by aural techniques on a clear night. Also shown is the typical pattern of hour-to-hour variation in the tracking ratio of migrants observed on radar.

from the radar data and projected the flight paths of migrants through a hypothetical night's migration on two typical clear nights, one in fall and one in spring. Data on which this extrapolation is based are the track directions of bird targets and their speeds, and the temporal pattern of migration for the particular night. Two related sets of observations support the validity of such an extrapolation: (1) The wind conditions which night migrants in this region appear to choose for migration are such that the air mass in which the birds are flying is moving (albeit at a slower rate) along with the birds (Graber and Cochran, 1960:260–262; Hassler et al., 1963: 61–63). This circumstance would appear to help the birds maintain their true courses. (2) The telemetered flights of two individual thrushes recorded in spring, 1965 (Anon., 1965; Graber, 1965) showed that birds tended to maintain their initial departure courses throughout the night, though on slightly curving paths.

I have used the term "migrant swarm" to designate the mass of migrating birds passing over a fairly large area. The term does not imply homogeneity in the species composition or uniformity of behavior of the migrating birds. In discussing directional patterns of migration and the composition of the migrant swarm, I have utilized species data from bird kills at television towers, thereby emphasizing the fall data: large kills are much less frequent in spring than in fall in this region.

From field observations reported in the literature I have attempted to determine the major fall migration routes for species of long-range night migrants which pass through east-central Illinois. Some of these data are summarized in Table 2. The principal references used in this summary were: for South Carolina: Sprunt and Chamberlain (1949); Georgia: Burleigh (1958); Florida: Sprunt (1954); West Indies: Bond (1961): Alabama: Imhof (1962); Louisiana: Lowery (1955); Mexico: Blake (1953); and Honduras: Monroe (1964).

Because the radar data for a given night may represent many different populations of birds, references to the mean track and other statistics may be of questionable validity, yet as an indication of the distribution of tracks and their variation from place to place and time to time, statistics (standard deviation, mean and standard error) are presented for most of the data samples included. In this paper statistical correlations or differences are considered significant at the 0.05 level or better.

Scientific names have not been included in this paper: nomenclature follows the A.O.U. Check-List of North American Birds, 5th Ed.. 1957.

COMPARISON OF RADAR AND AURAL RECORDS

Hourly variation.—On clear nights, the typical pattern of migration as seen on radar shows a peak in the number of migrants occurring shortly before midnight; the aural record indicates that the peak in the night's migration comes *after* midnight, usually just before dawn. By recording flight calls and radar targets simultaneously at the same place (Fig. 2), we can demonstrate that the difference in patterns probably reflect something other than the numbers of birds flying. Data for the night of 20–21 September 1960 are exemplary (Fig. 2). The radar showed that most of the migrants passing Champaign were at altitudes between 2,200 and 3,200 feet, well within the range of our audio system (Graber and Cochran, 1959:228). Species which I could identify with certainty from the tape were Swainson's Thrushes, Gray-cheeked Thrushes, and Dickcissels.

Cloud cover has a notable effect on the pattern of calling of night migrants. See Figure 3 for the overcast night of 19–20 September 1960. The record for this night shows the expected pre-dawn peak in calling, but it also shows conspicuously high peaks at other hours. Early in the night, migrants flying under complete overcast were extremely vociferous. As the cloud layer broke, calling declined, but as the overcast closed again about 2200 CST, calling began to increase again, though the radar showed fewer migrants present rather than more (Fig. 3). About midnight when a small number of migrants were under the overcast, the calling rate was high, but by 0200, when migrants appeared to be above the clouds, the calling rate had declined again just before the pre-dawn peak (Fig. 3). Ogden (1960: 65–66) noted the same phenomenon while making flight-call counts at a television tower in Tennessee. When complete overcast came in about mid-

TABLE 1
BIRDS KILLED IN SEPTEMBER (1957–1962) AT A TELEVISION TOWER IN CHAMPAIGN COUNTY, ILLINOIS.

Species	21–22 Sept. 1957 N	21–22 Sept. 1957 %	15–17 Sept. 1958 N	15–17 Sept. 1958 %	28–29 Sept. 1959 N	28–29 Sept. 1959 %	19–20 Sept. 1960 N	19–20 Sept. 1960 %	24–25 Sept. 1962 N	24–25 Sept. 1962 %	Totals N	Totals %
Swainson's Thrush	2	1.7	58	39.5	77	16.6	72	15.0	37	12.5	246	16.4
Ovenbird	32	28.1	4	2.7	66	14.2	85	17.7	31	10.5	218	14.5
Gray-cheeked Thrush	2	1.7	33	22.4	21	4.5	38	7.9	26	8.8	120	8.0
Magnolia Warbler	24	21.0	1	0.7	28	6.0	29	6.0	35	11.8	117	7.8
Red-eyed Vireo	4	3.5	13	8.8	42	9.0	49	10.2	4	1.3	112	7.5
Rose-breasted Grosbeak	1	0.9	2	1.4	39	8.4	29	6.0	21	7.1	92	6.1
Tennessee Warbler	8	7.0	5	3.4	25	5.4	21	4.4	16	5.4	75	5.0
American Redstart	4	3.5	—	—	13	2.8	23	4.8	27	9.1	67	4.5
Catbird	1	0.9	—	—	34	7.3	18	3.8	5	1.7	58	3.9
Bay-breasted Warbler	6	5.3	3	2.0	7	1.5	11	2.3	29	9.8	56	3.7
Chestnut-sided Warbler	4	3.5	1	0.7	17	3.7	12	2.5	7	2.4	41	2.7
Black and white Warbler	4	3.5	—	—	13	2.8	16	3.3	4	1.3	37	2.5
Yellowthroat	2	1.7	—	—	16	3.4	14	2.9	5	1.7	37	2.5
Bobolink	—	—	16	10.9	4	0.9	7	1.5	10	3.4	37	2.5
Scarlet Tanager	1	0.9	1	0.7	13	2.8	10	2.1	9	3.0	34	2.3
Philadelphia Vireo	5	4.4	1	0.7	8	1.7	11	2.3	4	1.3	29	1.9
Palm Warbler	1	0.9	—	—	6	1.3	3	0.6	5	1.7	15	1.0
Black-throated Green Warbler	1	0.9	—	—	3	0.6	5	1.0	4	1.3	13	0.9
Blackpoll Warbler	2	1.7	1	0.7	2	0.4	2	0.4	5	1.7	12	0.8
Northern Waterthrush	—	—	—	—	5	1.1	5	1.0	1	0.3	11	0.7
Wood Thrush	—	—	1	0.7	6	1.3	1	0.2	2	0.7	10	0.7
Blackburnian Warbler	2	1.7	1	0.7	3	0.7	3	0.6	1	0.3	10	0.7
Veery	—	—	4	2.7	3	0.6	1	0.2	—	—	8	0.5
Connecticut Warbler	—	—	—	—	2	0.4	4	0.8	2	0.7	8	0.5
Short-billed Marsh Wren	—	—	—	—	6	1.3	—	—	—	—	6	0.4
Long-billed Marsh Wren	2	1.7	—	—	2	0.4	2	0.4	—	—	6	0.4
Yellow-throated Vireo	—	—	2	1.4	—	—	1	0.2	1	0.3	4	0.3
Cape May Warbler	3	2.6	—	—	—	—	1	0.2	—	—	4	0.3
Black-billed Cuckoo	—	—	—	—	—	—	1	0.2	1	0.3	2	0.1
Eastern Wood Pewee	2	1.7	—	—	—	—	—	—	—	—	2	0.1
Brown Thrasher	—	—	—	—	2	0.4	—	—	—	—	2	0.1
White-throated Sparrow	1	1.7	—	—	1	0.2	—	—	—	—	2	0.1

TABLE 1 (*Cont.*)

Species	21–22 Sept. 1957 N	%	15–17 Sept. 1958 N	%	28–29 Sept. 1959 N	%	19–20 Sept. 1960 N	%	24–25 Sept. 1962 N	%	Totals N	%
Virginia Rail	—	—	—	—	—	—	1	0.2	—	—	1	0.1
Sora	—	—	—	—	—	—	—	—	1	0.3	1	0.1
Yellow-bellied Sapsucker	—	—	—	—	—	—	—	—	1	0.3	1	0.1
Traill's Flycatcher	—	—	—	—	1	0.2	—	—	—	—	1	0.1
House Wren	—	—	—	—	—	—	1	0.2	—	—	1	0.1
Nashville Warbler	—	—	—	—	—	—	—	—	1	0.3	1	0.1
Yellow Warbler	—	—	—	—	—	—	—	—	1	0.3	1	0.1
Myrtle Warbler	—	—	—	—	—	—	1	0.2	—	—	1	0.1
Savannah Sparrow	—	—	—	—	—	—	1	0.2	—	—	1	0.1
Totals	114	100.5	147	100.1	465	99.9	478	99.3	296	99.6	1,500	100.1

night his call count increased greatly but as the cloud layer broke the count declined again. Inherent in the observation that calling rate of migrants appears to vary with cloud conditions, is the question of whether the rate of calling is related to disorientation.

At Champaign on the overcast night, as on the clear night, *Hylocichla* thrushes accounted for about 80 per cent of the calls heard, yet that night 32 species of birds were killed at a TV tower just 11 miles from the radar-audio station and *Hylocichla* thrushes accounted for only about 23 per cent of the 478 birds killed (Table 1). The radar showed no migrants under 1,500 feet at any hour of the night (Fig. 3), despite the large number of birds killed at the 983-ft. tower.

The Tracking Ratio.—The hourly measure of the tracking ratio of migrants observed by radar may help to indicate what the birds are doing at a particular time of the night. In Figures 2 and 3, the tracking ratio is expressed as the per cent of bird targets making a track. This percentage rarely falls below 15 or reaches above 55. The tracking ratio pattern shown in Figure 1 is typical for a clear night. Early in the night the number of birds tracking is relatively low (about 28 per cent). The percentage climbs progressively until about the middle of the night, when nearly half the bird targets are tracking, and then progressively declines until at dawn the percentage is back to the low of around 30. Presumably the low figures at the beginning and end of the night reflect the fact that large numbers of migrants are changing altitude at these hours, ascending early in the night, descending late. It is in the middle of the night that the largest numbers of migrants maintain constant altitude. What I have interpreted to be altitudinal changes

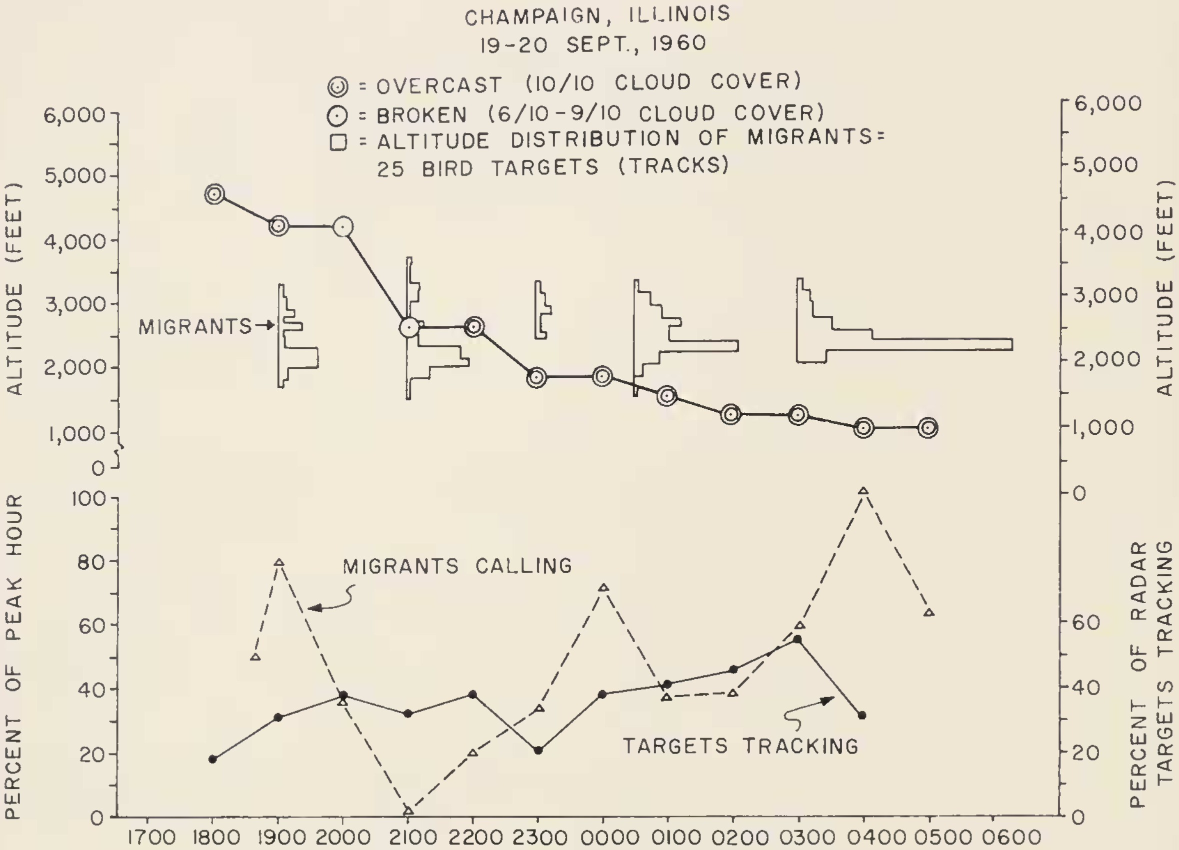

Fig. 3. Hour-to-hour variation in patterns of calling and tracking by migrants on an overcast night. Circle symbols and heavy line show altitude of cloud cover. Open square symbols show altitude and number of migrants.

could also be directional changes, for if migrants were changing their flight directions erratically early in the night and again late, the effect on the tracking ratio curve would be the same. For a clear night at least, it seems more reasonable to interpret the curve in terms of altitudinal, rather than directional shifts.

Under overcast on the night of 19–20 September 1960, birds departing from the Champaign area showed an exceptionally low tracking ratio (about 18 per cent, Fig. 3), and the hourly variation did not show the characteristic pattern seen on clear nights. As the cloud layer broke, the tracking ratio improved, but declined sharply when overcast reformed and lowered to 1,700 feet. As large numbers of migrants appeared above the overcast, the tracking ratio again improved before falling off about dawn, apparently as migrants started to land (Fig. 3). On this night birds were apparently shifting altitude, direction, or both, in response to changing cloud conditions.

There is also a possible non-ornithological explanation for the variation in the tracking pattern. If false echoes were particularly numerous early in the night and again late, the tracking pattern would be similar to that shown in Figure 2, because false echoes never make a track. This explanation does

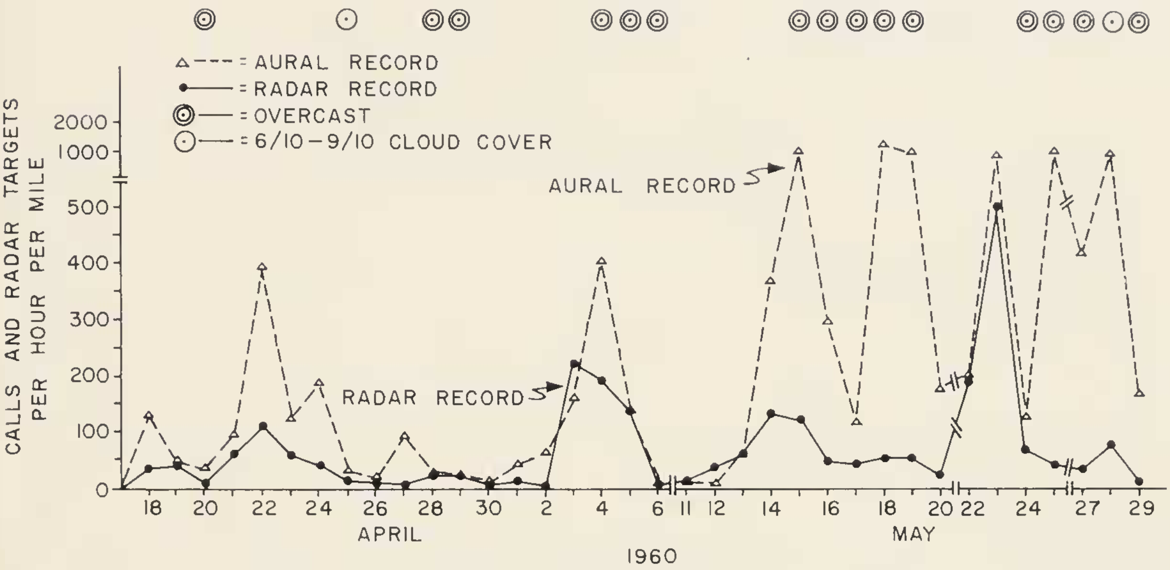

Fig. 4. Comparison of radar and aural records of migration at Champaign, Illinois, Spring, 1960.

not hold up under closer scrutiny however, because it is the number of tracking targets which actually effect the curve, while the number of non-tracking targets tends to remain more constant from hour to hour.

Nightly variation.—Because both radar and flight call counting are methods commonly used for the study of migration, it is worthwhile to directly compare seasonal radar and audio records made at the same time and place (see Fig. 4). There is no significant statistical correlation between the radar and aural readings from night to night ($r = 0.373$), though there is some coincidence of peaks in the graph (Fig. 4). As expected the aural record is more variable than the radar record. Because migrants are especially vociferous on overcast nights, it is not surprising that the disparity in results from the two techniques is particularly great on nights with cloud cover (Fig. 4).

SPECIES COMPOSITION OF THE MIGRANT SWARM

In the ensuing discussion tower kill data are used to indicate the species composition of the migrant swarm. It is, therefore, essential to ask how well the kills reflect the migrant fauna which we observe in the field. As a basis for comparison we have the results of field censuses conducted almost daily in Champaign County by Jean Graber and the author in forest and shrubby forest edge habitat during fall (14 August–15 October), 1957–1962, and spring (15 March–1 June), 1958 to 1963. A comparison of field count and tower kill figures for forest and forest edge species is presented in Figure 5. The data shown are the summed counts of birds killed, and birds seen in the field during the period (15–30 September, 1957–1962) when kills occurred.

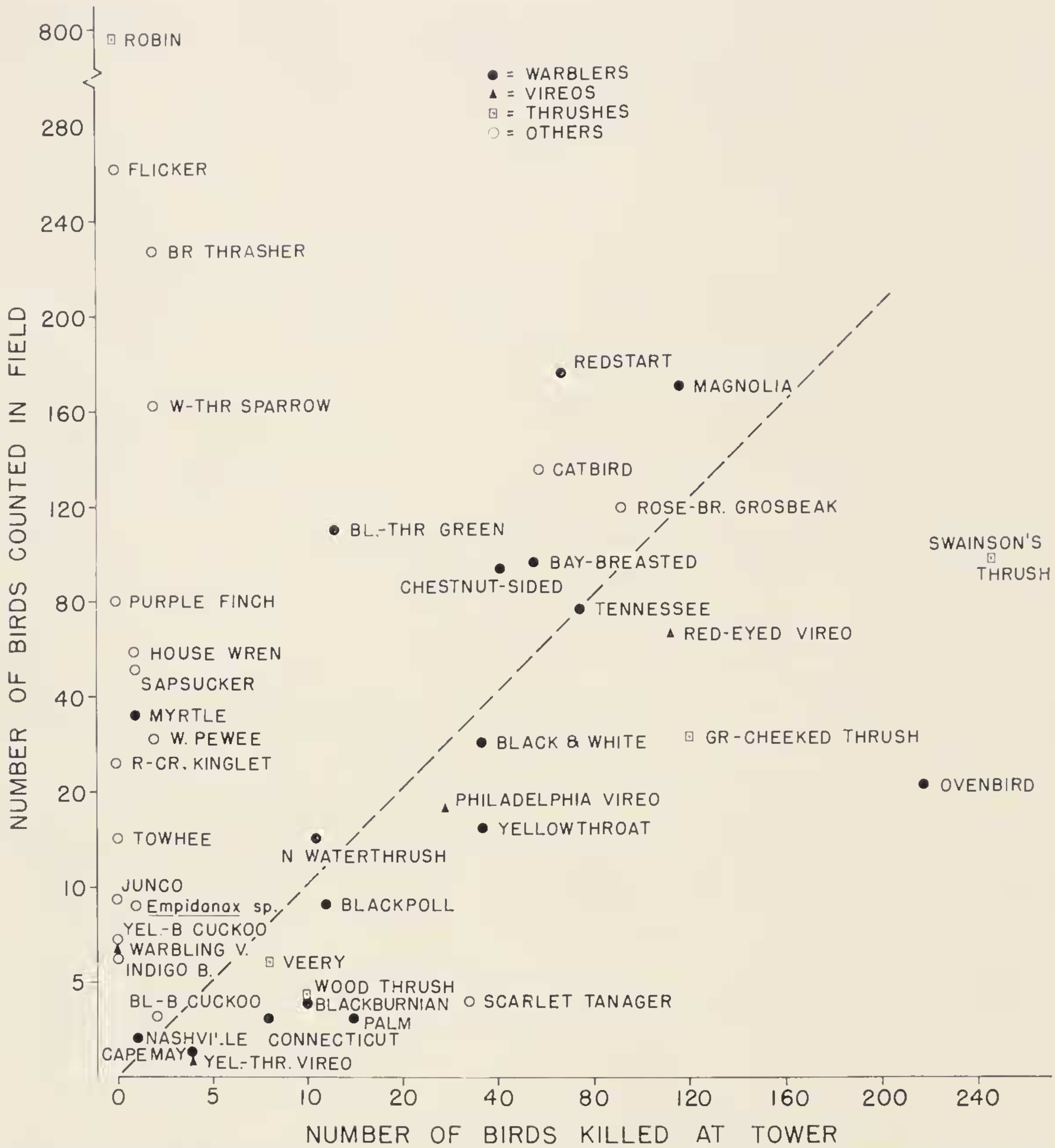

FIG. 5. Comparative data on the numbers of migrants killed at a television tower and the numbers observed in the field near Champaign, Illinois during the period (15–30 September 1957–1962) when kills occurred.

In general, species which were seen commonly in the field were also common tower victims, though there were notable exceptions. If we compare the number of birds of each forest species killed on a given night with the numbers of the same species counted in nearby woods the following morning, we find no significant correlation (r = 0.350) between the two counts. Further analysis shows that this lack of correlation largely reflects the field observer's varying ability to see different species in their natural habitat. Inconspicuous species (Ovenbird, Gray-cheeked Thrush) are killed in numbers out of proportion to the numbers seen, while conspicuous species (flycatchers. Myrtle Warbler) *seem* to be less frequent victims. If we choose closely related species and compare the numbers killed with the numbers seen, we usually find a high degree of correlation between the counts. For example, correlation coefficients between field counts and kill counts for species of vireos (r = 0.993), *Hylocichla* thrushes (r = 0.983), and *Dendroica* warblers (r = 0.828) are all significant. Some of the discrepancies are inexplicable. One *Dendroica*, the Black-throated Green Warbler, appears to be much less susceptible to the tower peril than its congeners (Fig. 5). The Robin, seen in greater numbers than any other species during the kill period, has not been recorded as a casualty. The Robin is widely known as a diurnal migrant, though in east-central Illinois arriving flocks often seem to appear during the night or very early morning. Yellow-shafted Flickers were more numerous during the September kill period than at any other time, yet the few flickers we have found at the tower were killed in early October. Does this imply that some flicker populations are more susceptible to kill than others?

The September tower kills at Champaign include relatively few open field species (Table 1): most of the open field passerine migrants pass through the area after September. Stoddard's (1962) study showed that the open field fringillids and other passerines are also common tower victims during their late fall migrations. Shorebirds and waterfowl pass mainly either before or after September, though shorebirds and waterfowl appear to be relatively rare casualties at any U. S. tower at any season.

While this analysis provides justification for using kill data to interpret the September directional patterns of migration observed at Champaign, it should be remembered that the altitude range covered by the tower is entirely different from that covered by radar; this discrepancy could represent important faunal differences.

DIRECTIONAL PATTERNS OF MIGRATION

Investigators who use radar in migration studies often average their directional data to obtain a generalized picture (Bellrose and Graber, 1963: 366; Drury and Nisbet, 1964:70, and others). This procedure is useful, and is applied in the present study also, but it presents an overly simplified picture. On any given night during the migration seasons, many species of birds are flying (Table 1; see also Brewer and Ellis, 1958), and each species may represent a number of distinct populations (Raveling, 1965:91). Thus, the great spread of track directions recorded by Champaign radar during one night (Figs. 6 and 7) is not surprising. As yet there is no way to ascribe the various tracks observed on our radar to particular species or populations of birds, though this is probably an attainable goal.

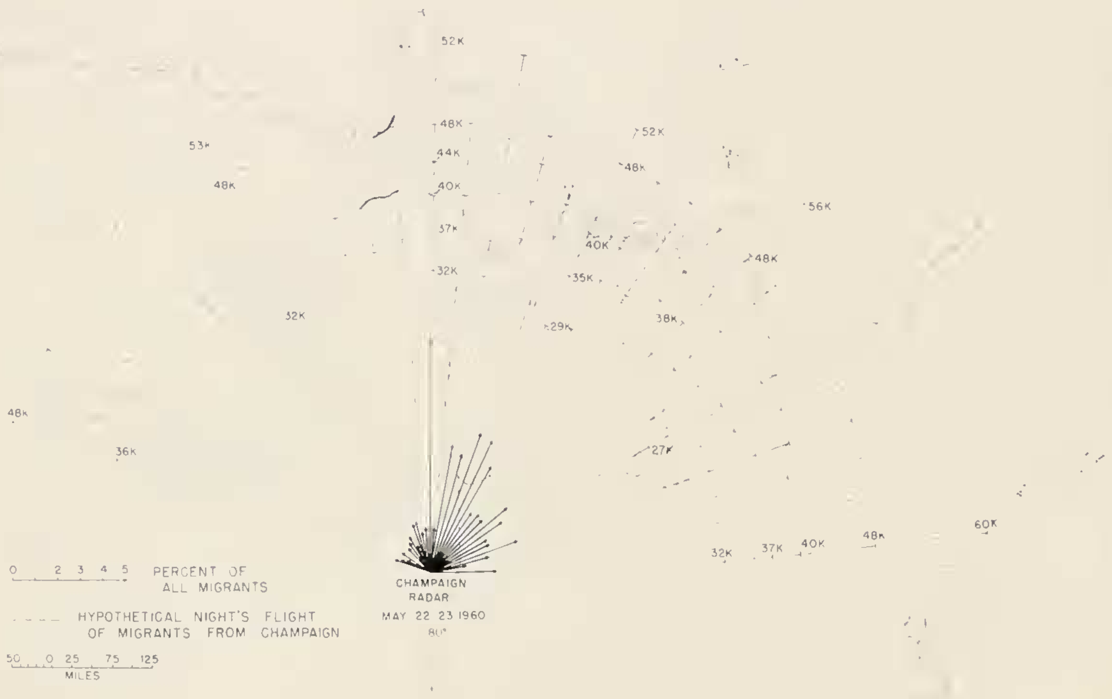

FIG. 6. Flight directions of migrants recorded by radar on a typical clear Spring night. Heavy arrows show the per cent of migrants on a given 5-degree track. Dash lines extend the radar tracks through a full night's migration, the extrapolation based on each track direction, its speed in knots (K), and the temporal pattern observed at Champaign.

As observed by radar, there is a typical pattern of flight directions for the long-range passerine migrants which pass through central Illinois in large numbers particularly in May (Fig. 6) and September (Fig. 7). On an exemplar spring night (22–23 May 1960) about 75 per cent of the migrants were tracking east of 355 degrees (Fig. 6). Projected, the majority of these tracks intersect the belt of coniferous forest between the Great Lakes and Hudson Bay, the center of the breeding range for many of the northern migrants which pass Champaign at this season. The audio record for this night showed the presence of Swainson's and Gray-cheeked thrushes, cuckoos, Dickcissels, and Solitary Sandpipers, plus other species, probably mainly northern warblers, whose call notes I could not identify specifically. Because most of the species of long-distance migrants which are common in the Champaign area in spring, also appear there commonly in fall, we might expect that the spring and fall directional patterns detected by Champaign radar would simply be reversed in the two seasons, i.e., with the dominant vectors northeast in spring and southwest in fall. In fact, the dominant vectors are east of the north-south line in *both* spring and fall (Figs. 6, 7 and 9).

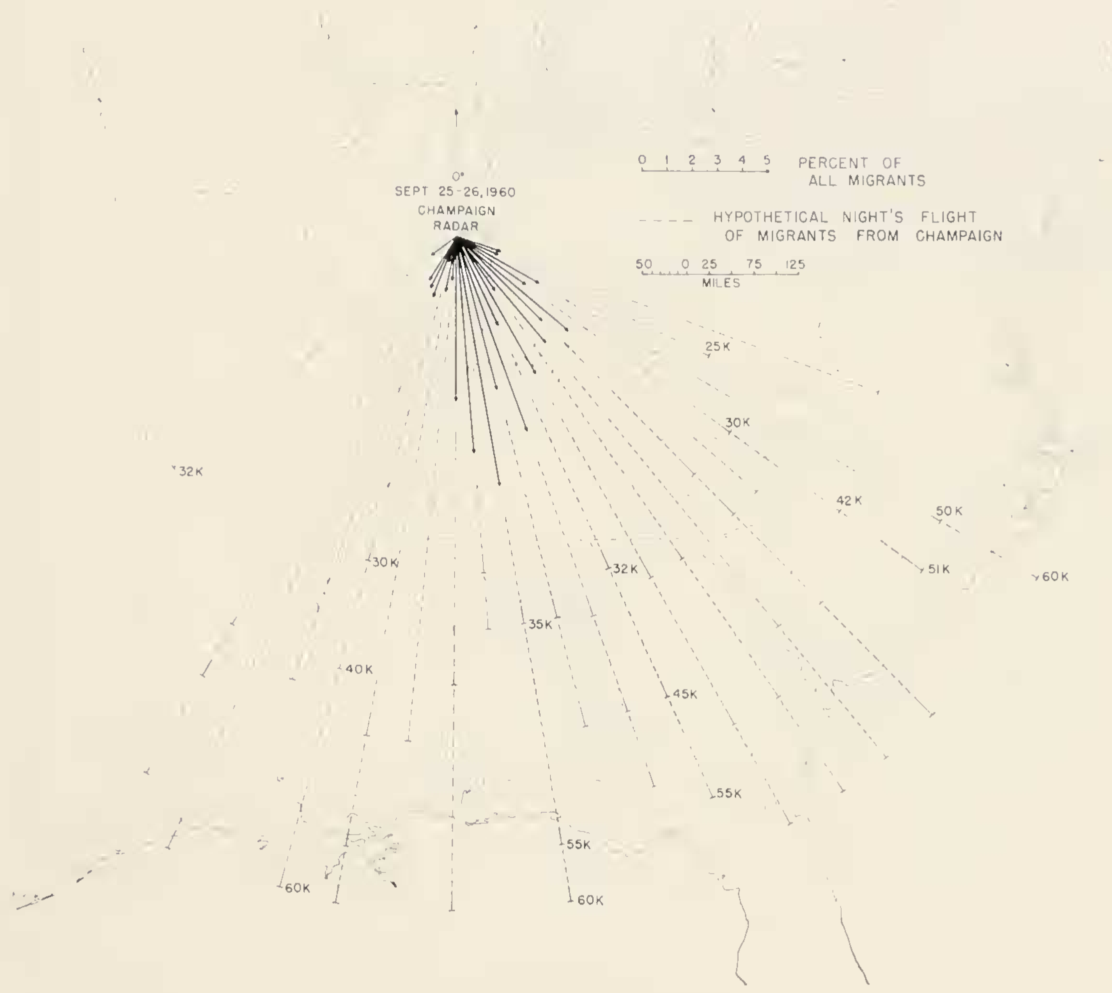

FIG. 7. Flight directions of migrants recorded by radar on a typical clear Fall night. Heavy arrows show the per cent of migrants on a given 5-degree track. Dash lines extend the radar tracks through a full night's migration, the extrapolation based on each track direction, its speed in knots (K), and the temporal pattern observed at Champaign.

Characteristically for fall, on the exemplar night of 25–26 September 1960 about 75 per cent of the bird targets detected by Champaign radar were tracking east of south (180 degrees), with only 18 per cent west of south, and only 6 per cent aimed west of the Gulf of Mexico (Fig. 7). Thus, nearly all of the long-distance migrants which pass Champaign at this season appear to be en route either to a trans-Gulf or a Florida-Antillean (West Indies) migration, or some combination of the two. Most of these night migrants are of species which winter in Central or South America or the West Indies. Their probable fall migration routes can be ascertained from data presented in various regional studies (Table 2). Migrants tracking east of 165 degrees from Champaign would intercept either the Florida peninsula or the southern U. S. Atlantic coast (Fig. 7), and would appear to

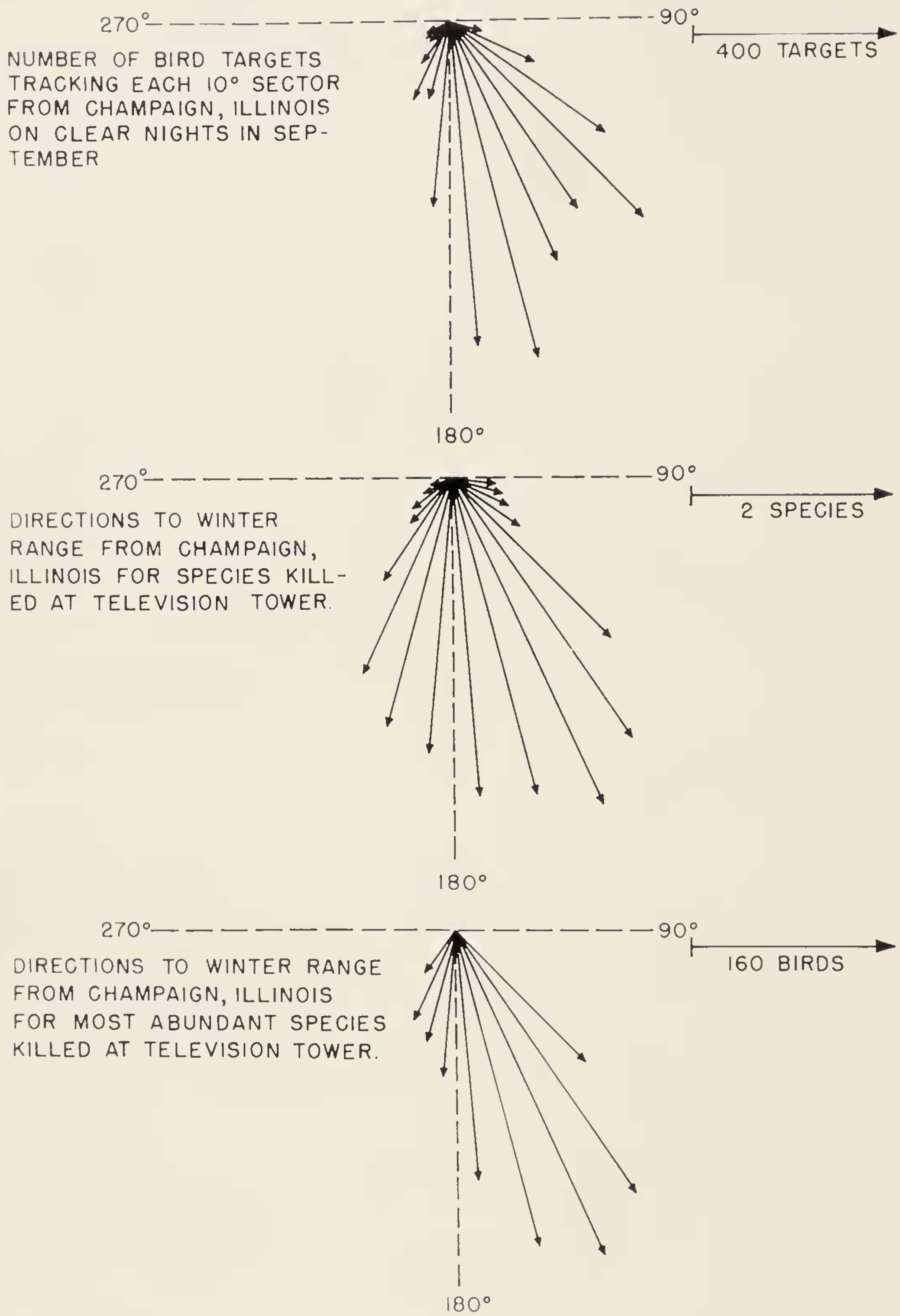

Fig. 8. Comparative data on the number of bird targets tracking each direction from Champaign radar (top), the directions to the winter ranges from Champaign for species of night migrants killed at Champaign (middle), and the directions of the winter ranges for the most abundant species of migrants killed at Champaign (bottom).

TABLE 2
DATA ON PROBABLE FALL MIGRATION ROUTES OF SPECIES OF LONG RANGE MIGRANTS KILLED AT CHAMPAIGN, ILLINOIS.

Species	South Carolina	Georgia	Florida	West Indies	Alabama	Louisiana	East-Central Mexico	Honduras	Kill Ratio 1 Bird Ill. : N Florida	Primary Route(s)
Gray-cheeked Thrush	+	+	0	0	+	+	0	0	0.4	Tr.-Gulf
Veery	+	0	0	0	0	+	0	0	52	"
Philadelphia Vireo	0	0	0	0	0	+	0	+	0.1	"
Chestnut-sided Warbler	+	+	0	0	+	+	0	+	4	"
Scarlet Tanager	0	+	+	0	+	+	0	0	1	"
Traill's Flycatcher	0	0	0	0	0	+	+	+	5	Tr.-Gulf &
Wood Thrush	+	+	0	0	+	+	+	+	9	Mexico
Swainson's Thrush	+	+	0	0	+	+	+	+	0.5	"
Yellow-throated Vireo	+	+	+	0	+	+	+	+	14	"
Red-eyed Vireo	+	+	+	0	+	+	+	+	14	"
Blackburnian Warbler	+	+	0	0	+	+	+	+	4	"
Nashville Warbler	0	0	0	0	0	+	+	0	1	"
Bay-breasted Warbler	0	+	0	+	+	+	0	+	1	W. Ind.-Tr.-G
Cape May Warbler	+	0	+	+	0	0	0	0	0.5	W. Indies
Blackpoll Warbler	+	0	+	+	0	0	0	0	0.1	"
Palm Warbler	+	+	+	+	0	0	0	+	18	"
Bobolink	+	0	+	+	0	0	0	0	2	"
Black-billed Cuckoo	0	0	0	+	0	+	+	+	3	All Routes
Wood Pewee	+	+	0	+	+	+	+	+	5	"
Catbird	+	+	+	+	+	+	+	+	6	"
Black and white Warbler	+	+	+	+	+	+	+	+	4	"
Tennessee Warbler	0	+	0	+	+	+	+	+	1	"
Yellow Warbler	+	+	+	+	+	+	+	+	23	"
Magnolia Warbler	+	+	0	+	+	+	+	+	1	"
Myrtle Warbler	+	+	+	+	+	+	+	+	4	"
Black-throated Green Warbler	0	+	0	+	+	+	+	+	0.7	"
Ovenbird	+	+	+	+	+	+	+	+	0.8	"
Northern Waterthrush	0	+	+	+	+	+	+	+	11	"
Yellowthroat	+	+	+	+	+	+	+	+	8	"
American Redstart	+	+	+	+	+	+	+	+	4	"
Rose-breasted Grosbeak	0	0	0	+	+	+	+	+	0.1	"

Sources of data are given in the text. Symbol + indicates the species is fairly common to abundant as a transient or winter bird; symbol 0 indicates uncommon, rare or absent at the particular locality.

be en route to an Antillean migration. Tracks which fall in this sector comprise about 60 per cent of the tracks detected by Champaign radar in mid- to late September. Coincidentally, about 60 per cent of the migrants killed at Champaign tower in this period are of species which appear commonly in the Antilles either as transients or winter birds (Tables 1 and 2). Other species of migrants which are frequent tower victims in September rarely appear in the Antilles (Table 2); they comprise about 40 per cent of the birds killed at Champaign, and coincidentally, about 40 per cent of the tracks picked up by Champaign radar are aimed at the Gulf of Mexico west of the Antilles.

The directional pattern of migrants at Champaign could also be expected to have a direct relationship to the destinations (winter ranges) of the

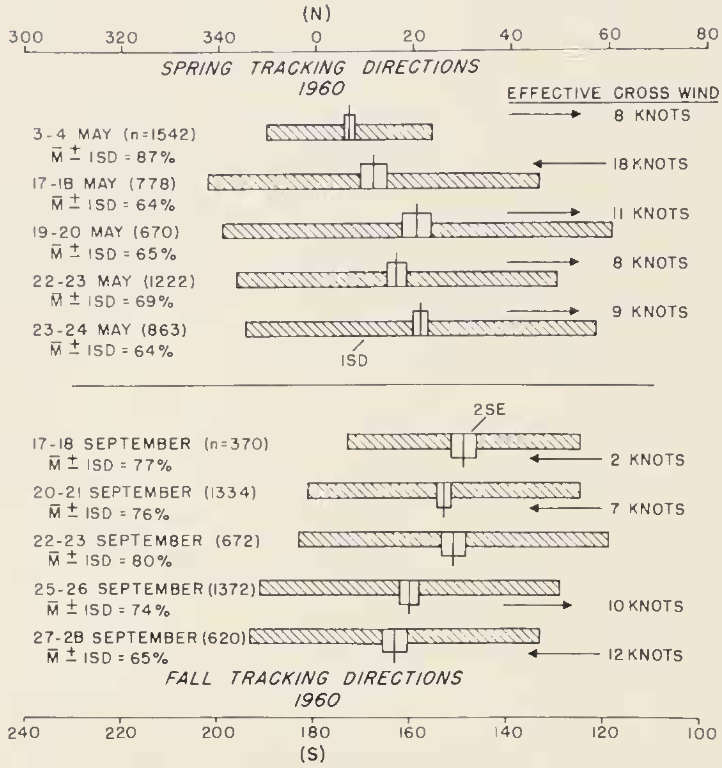

FIG. 9. Distribution of tracking directions (in degrees) of migrants from Champaign, Illinois on clear nights in spring and fall. The vertical line represents the mean track, the center box represents 2 standard errors on each side of the mean, and the lateral shaded boxes represent 1 standard deviation on each side of the mean. The effective crosswind was calculated for the group of migrants representing the mean track and speed, using winds aloft data for central Illinois.

migrants involved. The longitudinal breadth of the winter range varies greatly between different species of migrants. For example, the known winter range of the Red-eyed Vireo lies between eastern Ecuador on the west and southwestern Venezuela on the east (A.O.U. Check-list, 1957). To reach this area in the shortest flight distance (Great Circle Route) from Champaign, vireos should fly a course between 163 and 148 degrees from Champaign, an arc of 15 degrees. The winter range of the Ovenbird is much broader, lying between 219 and 131 degrees from Champaign, an arc of 88 degrees. By plotting the tracking arcs that represent the Great Circle Route to the wintering grounds of common night migrants in this area, we can determine precisely where the winter ranges for these species are in relation to Champaign, and compare the winter range directions with the flight directions recorded by radar (Fig. 8). From this analysis, it is clear that the winter ranges of the species killed at the Champaign television tower lie predominantly east of the Champaign meridian (88 deg. 15 min.), and that there is a high degree of correlation ($r = 0.895$) between the directions to the winter ranges and the radar directional pattern (Fig. 8). The winter ranges

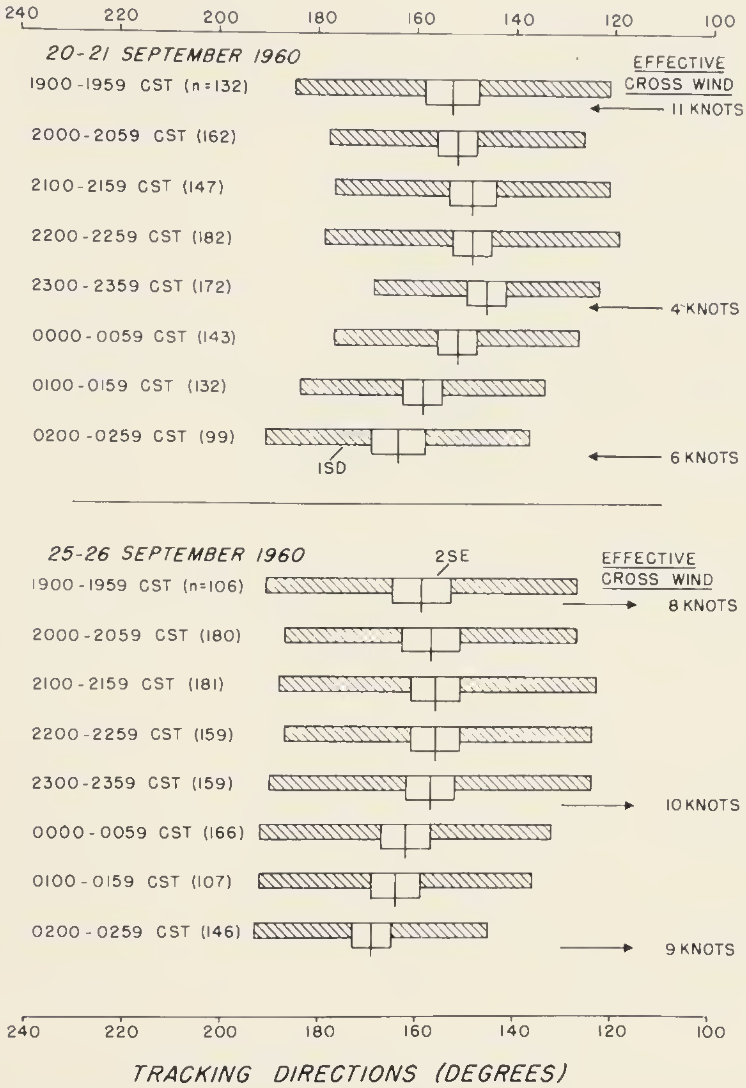

FIG. 10. Variation in tracking directions of migrants from hour to hour on two clear Fall nights, as observed by radar at Champaign, Illinois. The vertical line represents the mean track, the center box represents 2 standard errors on each side of the mean, and the lateral shaded boxes represent 1 standard deviation on each side of the mean.

of the most common species killed (Table 1) are even more decidedly easterly (Fig. 8).

NIGHTLY, HOURLY AND LOCAL VARIATION IN THE DIRECTION OF MIGRATION

The concept of a typical directional pattern of migration for an area, though useful as a generalization, is still an oversimplification. Even on clear nights the recorded flight directions actually showed significant variation from night to night (Fig. 9, Table 3), and even from hour to hour (Fig. 10, Table 3). There was no consistent relationship between variation in the directional pattern and variation in wind direction or speed (Figs. 9 and 10).

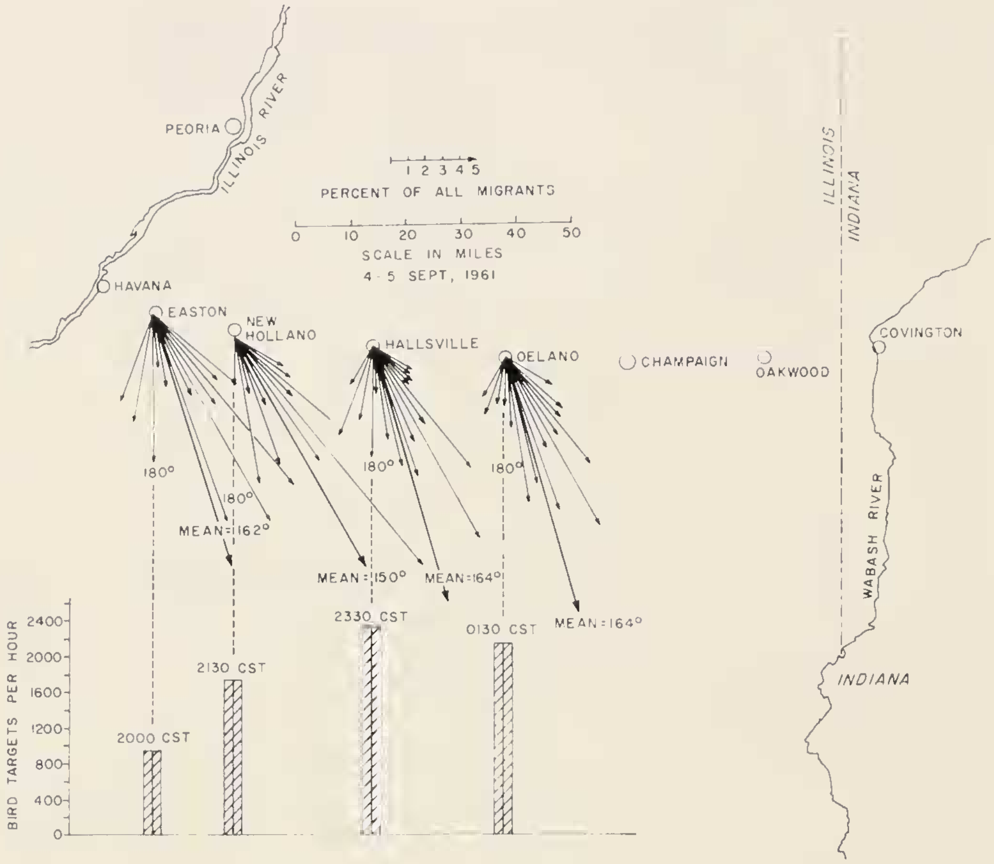

Fig. 11. Flight directions and numbers of night migrants at four localities in central Illinois on the night of 4–5 September 1961, as observed with a mobile radar unit.

Both in spring and fall there was also conspicuous variation in the spread of tracks. On most clear nights in spring about 65 per cent of the tracks fall within the range of the mean plus and minus 1 SD (Fig. 9), the track distribution in this respect resembling a normal distribution. A notable exception was the night of 3–4 May, when tracks were closely bunched around the mean (Fig. 9). Only a few of the calls recorded that night were identifiable (Dickcissels): the field censuses indicated a large flight of Palm Warblers and White-throated Sparrows, but little else. The mean flight direction on this night was less decidedly eastward than on other clear May nights, a fact probably relating to the position of the breeding range of the Palm Warbler (nominate race) which lies mainly west of the Champaign meridian. In general, tracks of migrants were more tightly bunched around the mean in fall than in spring (Fig. 9). This greater spread of tracks in spring is not surprising for the breeding grounds of most of the long distance migrants are only about 10 degrees of latitude north of Champaign, and have a broader longitudinal spread than the wintering grounds which lie about 25 degrees south from Champaign.

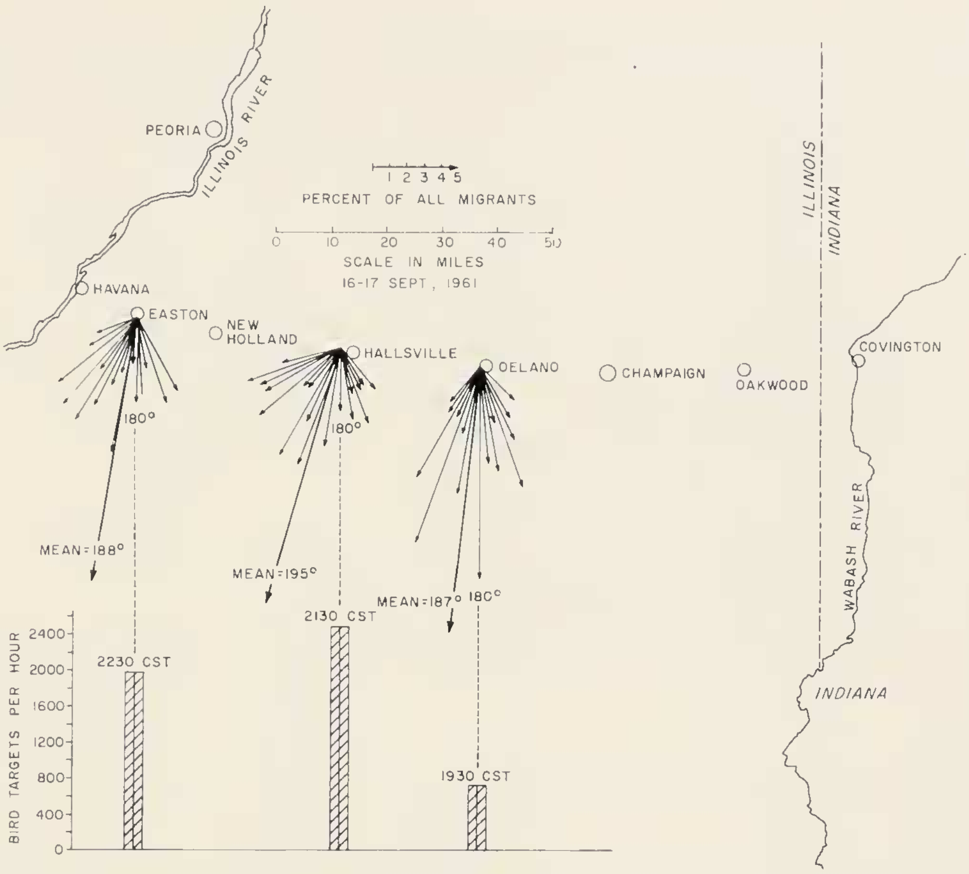

FIG. 12. Flight directions and numbers of night migrants at three localities in central Illinois on the night of 16–17 September 1961, as observed with a mobile radar unit.

Hour-to-hour variation in the September tracking pattern is generally insignificant in the hours before midnight, but significant changes occur after midnight, with the mean track often, but not invariably, turning westward (Fig. 10, Table 3). The cause and significance of this post-midnight change in the mean flight direction are unknown, but are not apparently related to wind variation, for on the nights examined, the winds aloft varied more before midnight than after (Fig. 10).

Having observed the flight directions of long-distance migrants at Champaign, I was interested in learning whether the flight patterns varied from one locality to another in central Illinois. The flight directions observed with the mobile radar unit at a few central Illinois localities on clear nights in September are shown in Figs. 11–13. The mobile radar is satisfactory for making rough comparisons of the flight *directions* of migrants at different localities, but the time difference in the data from any two or more stations complicates the comparison of flight *densities* between stations, because flight densities almost invariably change from hour to hour. Note in Figure 11 the flight densities at different stations seem to show the typical temporal pattern seen at a single station (see Fig. 2).

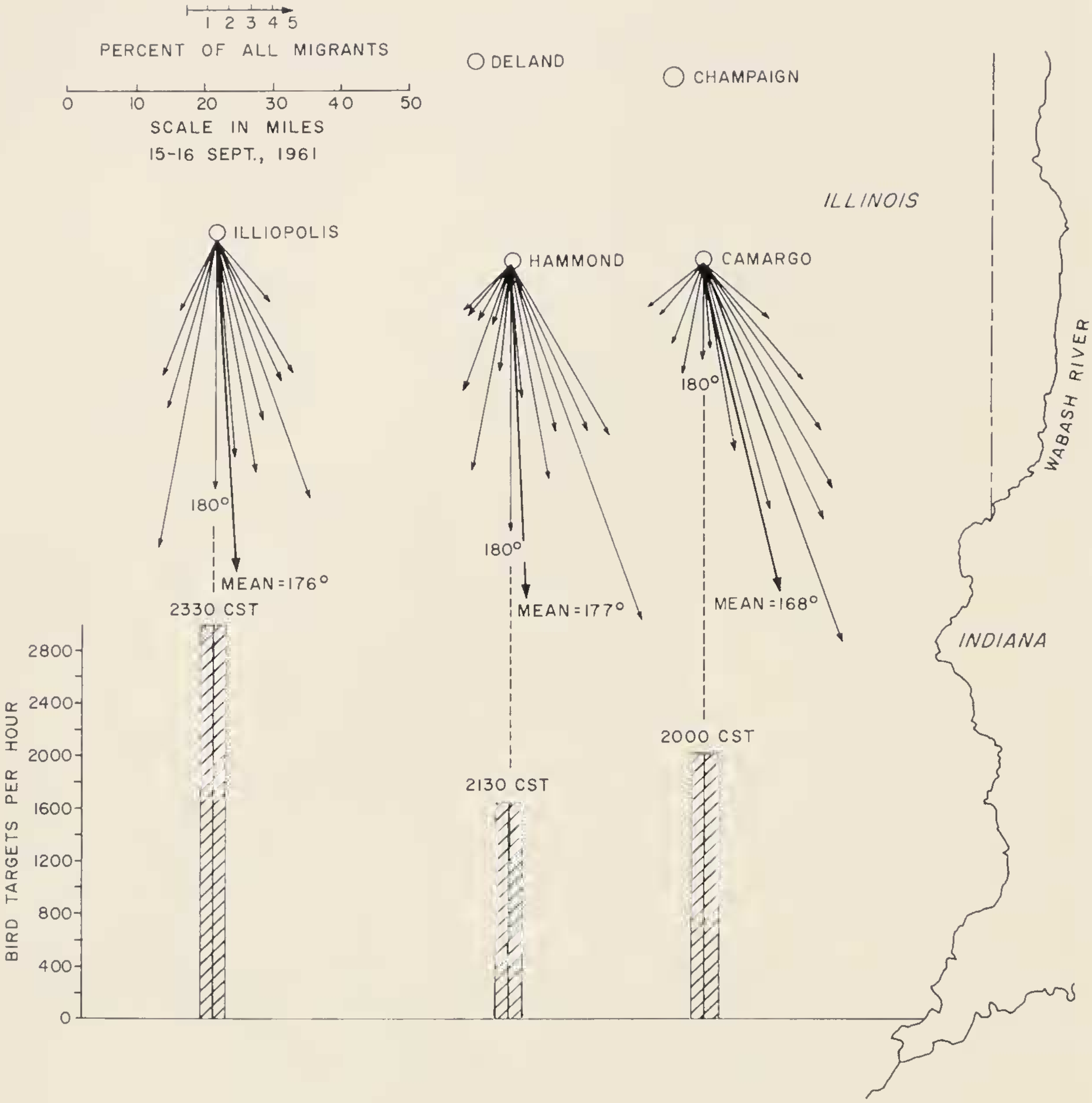

FIG. 13. Flight directions and numbers of night migrants at three localities in central Illinois on the night of 15–16 September 1961, as observed with a mobile radar unit.

On the night of 4–5 September 1961, the dominant flight directions showed the typical east-of-south pattern at all stations spanning a transect of about 80 miles (Fig. 11). The mean track at different stations varied from 150 to 164 degrees, more than the usual hourly variation (pre-midnight) at Champaign, but less than the variation observed between nights. Over the same region on the night of 16–17 September 1961 the dominant flight directions were *west* of south (the means: 187 to 195 degrees), but again the basic directional pattern was the same at all stations (Fig. 12). This west of south movement, exceptional for central Illinois, actually began the night before (15–16 September), and the mobile radar transect for that night shows its development (Fig. 13). As the mobile unit moved west, the tracks of migrants appeared to shift increasingly westward. This shift was not related to geography but to time, for the radar had detected a great influx of southwestward-oriented migrants whose numbers increased greatly after 2130 CST. This change in the flight direction pattern was *not* related to changing winds, for the wind conditions in central Illinois were almost identical (about 300 degrees at 10–15 knots for altitudes between 150 and 2,000 meters) on the two nights during which the change occurred. The southwestward direction of this flight, then, almost certainly related to the species composition of the migrant swarm. Field observations made on the morning of 17 September across central Illinois shed light on the species which were probably involved in the flight. Conspicuous among the arriving migrants were Black-crowned Night Herons, Common Nighthawks, American Coots, Yellow-shafted Flickers, Yellow-bellied Sapsuckers, Wood Pewees, *Empidonax* flycatchers, Catbirds, and Warbling Vireos. All but the flicker are common transients in Mexico, and all are likely candidates for a southwest migration from Champaign.

In general, the flight directions of September migrants as observed by radar over the Illinois River at Havana are similar to those observed at Champaign, though the mean nightly track at the two stations may differ significantly (Table 3). Weather may have a pronounced effect on the directional pattern of migration in central Illinois, as on the night of 24–25 September 1962. On this night the tracking pattern of migrants at Havana was the typical September pattern for central Illinois localities (Figs. 14 and 15). The mean track was 155 degrees (SD = 32 degrees); the range of mean ± one SD included about 75 per cent of all tracks observed. Early in the night (until 2130 CST) there was fog at Havana and visibility was poor, but there was no sustained overcast in the area. Most of the migrants that passed Havana were coming from the northwest where clearer weather conditions prevailed. No large scale bird kills occurred at high TV towers in Peoria and Moline (north and west of Havana radar). South and east of Havana, weather deteriorated and sizeable kills of migrants occurred at Springfield and Champaign (Figs. 14 and 16), where low overcast (under 3,000 feet) and fog persisted with low visibilities (under 4 miles) nearly all night. This weather accompanied a slow-moving cold front that reached Springfield and Champaign at about the same time (2130 CST). By midnight the front had moved only a few miles beyond Champaign. This is the typical combination of weather and migration patterns (large numbers of migrants overtaking a front) which precipitate kills in this region (Graber and Cochran, 1960:268). The flight direction pattern of migrants at Champaign was very different from the "normal" and from the pattern at Havana

TABLE 3

PROBABILITIES OF SIGNIFICANT DIFFERENCES IN THE TRACKING PATTERNS OF NIGHT MIGRANTS IN CENTRAL ILLINOIS FROM STATION TO STATION, FROM NIGHT TO NIGHT, AND FROM HOUR TO HOUR.

Localities–Dates–Hours	Probability of Significant Difference		
	Between Stations	Between Dates	Between Hours
Champaign			
20–21 Sept. 1960 (1900–2300 CST; 4 hours)			0.500
(2300–0300 CST; 4 hours)			0.999
22–23 Sept. 1960 (2000–2300 CST: 3 hours)			0.999
(2300–0300 CST; 4 hours)			0.500
25–26 Sept. 1960 (1900–0000 CST; 5 hours)			0.500
(0000–0300 CST; 3 hours)			0.900
Champaign			
19–20, 22–23, 23–24 May 1960 (3 nights)		0.990	
17–18, 20–21, 22–23 Sept. 1960 (3 nights)		0.950	
Easton Hallsville–Deland			
4–5 Sept. 1961	0.500		
16–17 Sept. 1961	0.800		
4–5, 16–17 Sept. 1961		0.995	
Champaign–Havana			
24–25 Sept. 1962	0.995		
25–26 Sept. 1962	0.800		
26–27 Sept. 1962	0.995		

(Figs. 14 and 15). The mean track at Champaign was 175 degrees (SD = 48 degrees), with nearly as many birds tracking west of south as east of south. The mean ± one SD included 63 per cent of the tracks observed. The high standard deviation, indicating a wide spread in the tracks, reflects a mass disorientation in the migrant swarm.

In numbers, the kills at Springfield (218 specimens) and Champaign (296 specimens) were not unusual for late September. The species composition of the kill was also typical for Champaign (Table 1). The kills at Champaign and Springfield were remarkably similar, even to the numbers of each species killed (Fig. 16). The most noteworthy differences in the kills at the two stations were in the larger numbers of *Hylocichla* thrushes, Magnolia Warblers, and Rose-breasted Grosbeaks killed at Champaign (Fig. 16). Data from another simultaneous kill (16–17 September 1958) at the two towers indicates that the species differences were not due merely to chance. The 1958 kill was much greater at Springfield (827 specimens) than at Champaign (117 specimens), possibly because visibility in the Springfield

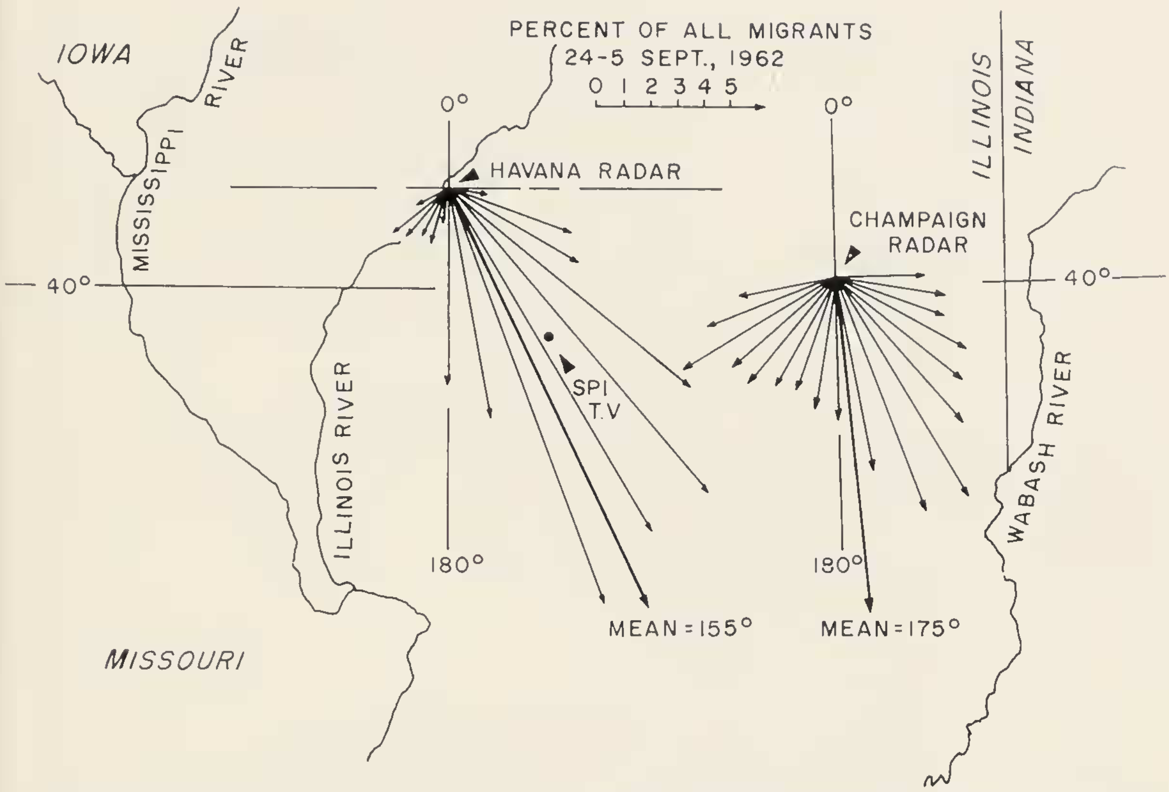

FIG. 14. Flight directions of migrants at Havana and Champaign, Illinois on night of 24-25 September 1962. Note the wide spread of tracks indicating deterioration of orientation at Champaign. Kills of migrants occurred at towers near Springfield (SPI) and Champaign.

area remained poor most of the night after midnight, while at Champaign visibility was poor only for about 1 hour (2300–0000 CST) during the night. Despite the disparity in total numbers of birds killed, the 1958 and 1962 kills at Champaign and Springfield showed the same general ties between species and locality (Fig. 17). On both dates, more thrushes and grosbeaks were killed at Champaign, while the Springfield tower claimed more Ovenbirds, Tennessee Warblers, Chestnut-sided Warblers, Bay-breasted Warblers, Northern Waterthrushes and Yellowthroats. Of the thirteen most numerous species killed (87 per cent of the total kill), only two (Magnolia Warbler and Bobolink) were not consistently more numerous at one tower than the other (Fig. 17). The probability of such a coincidence by chance is less than 0.02 ($\chi^2 = 6.23$, 1 df). These data indicate that each locality has its own characteristic fauna of passing migrants. In this observation there is also an implication that each population of migrants follows precisely the same migration route year after year.

DISCUSSION

An observer's impressions of night migration may vary considerably, depending upon the technique of study he uses. Vleugel (1960) discussed

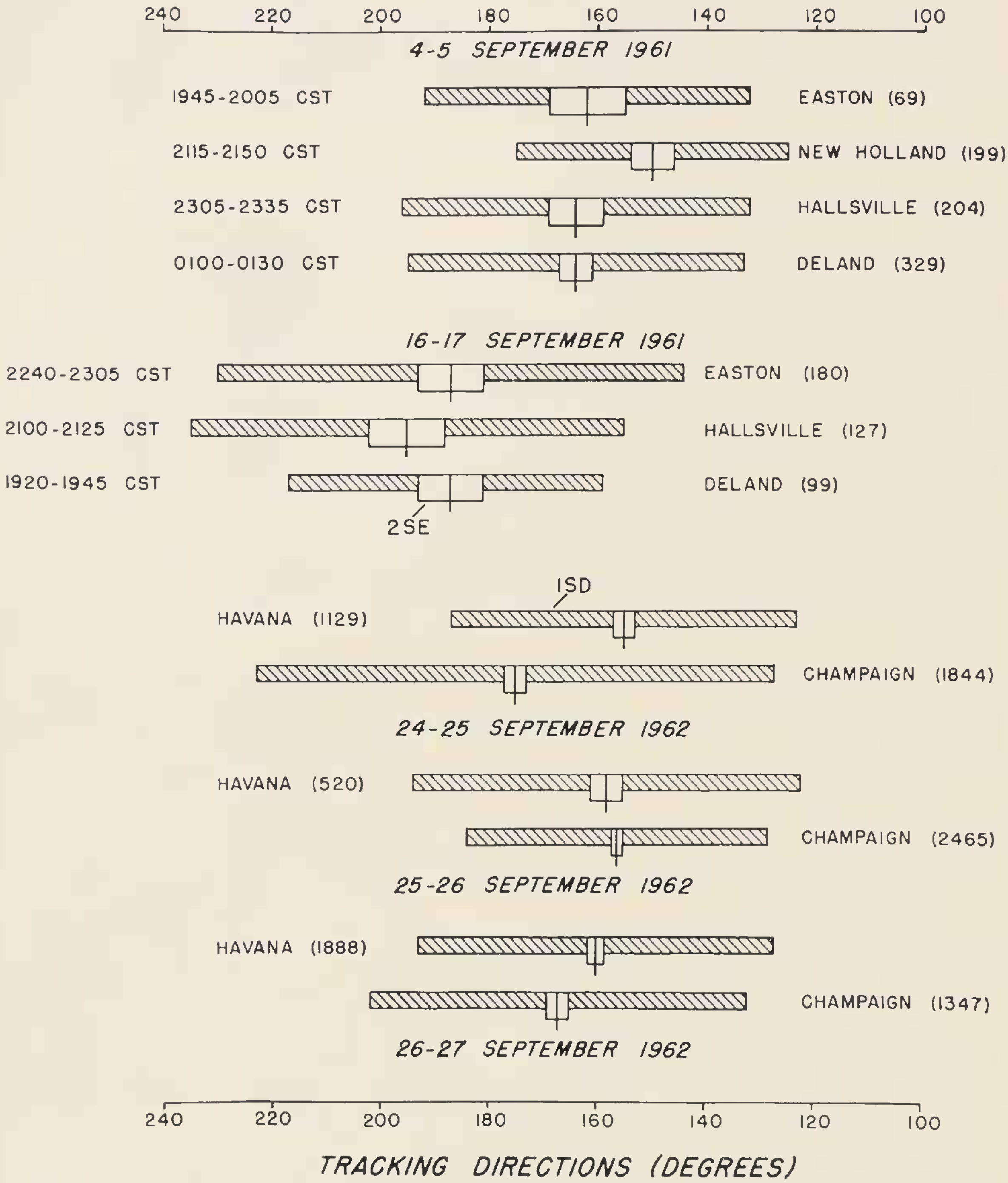

FIG. 15. Comparative data on the variation in flight directions of night migrants at various localities in central Illinois. Numerals in parentheses are the numbers of tracks recorded in each sample.

the contradictory findings from lunar and aural studies on the nightly temporal pattern of migration. Dwelling particularly on Ball's (1952) study of thrush migration on Gaspe. Vleugel (p. 15) hypothesized that the aural temporal pattern reported by Ball could be explained on the basis of geography (the sizable water barrier around Gaspe). In the flat farmlands of central Illinois, the pattern of migrant calling is the same as that which Ball

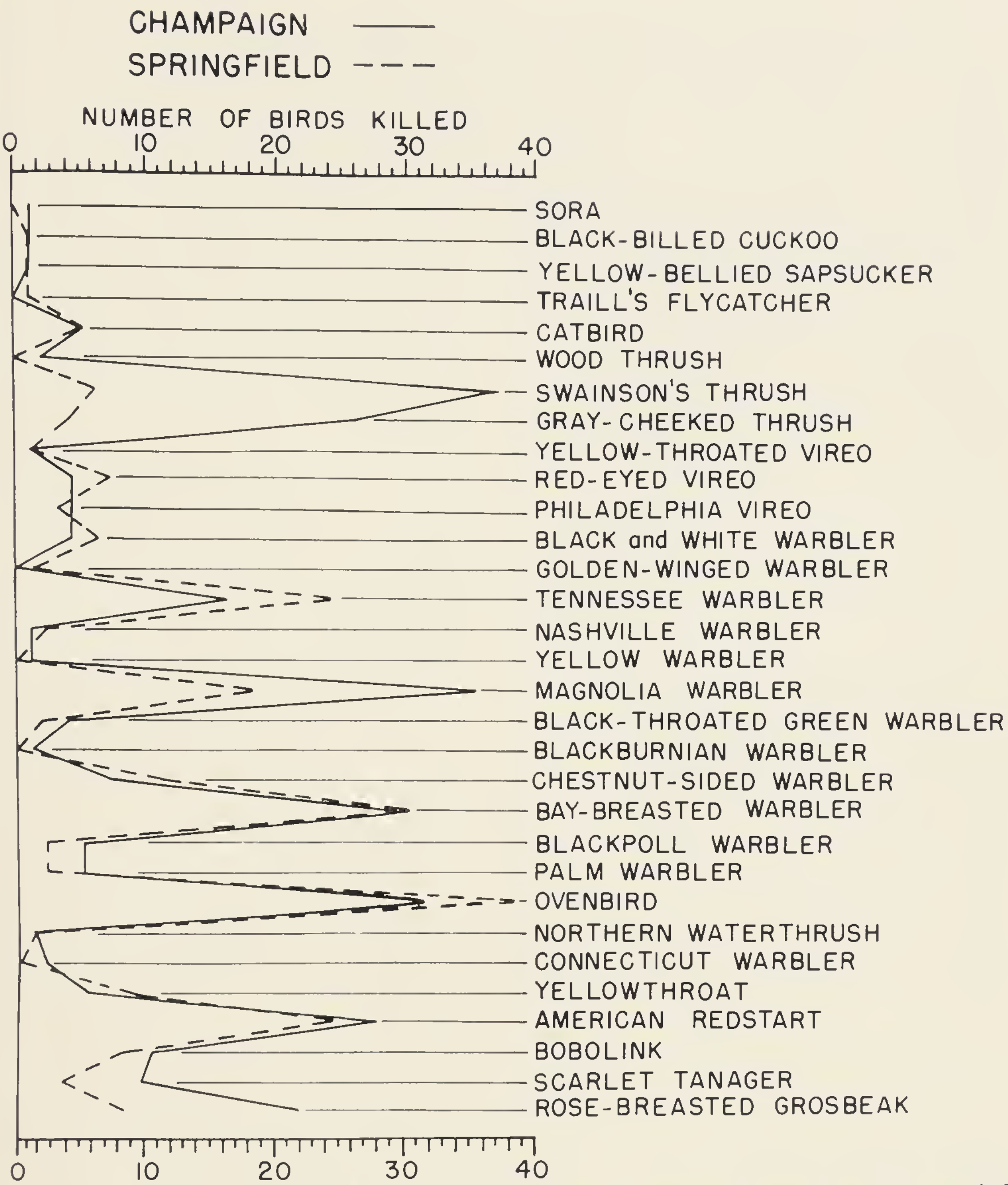

Fig. 16. Comparative numbers of migrants killed at television towers near Springfield and Champaign, Illinois on the night of 24–25 September 1962.

recorded in Quebec. Furthermore, the consistent nightly temporal pattern of migration as observed on radar in central Illinois is similar to the pattern recorded through lunar observations in many areas (Lowery, 1951:116; Hassler et al., 1963:57). Obviously, then, these typical patterns do not reflect topography or geography, but something that the birds themselves are doing. One technique seems to belie the other. When radar shows the number of migrants to be declining in the early morning, the audio system suggests that more migrants are calling. Radar shows that migrants are *not* flying at

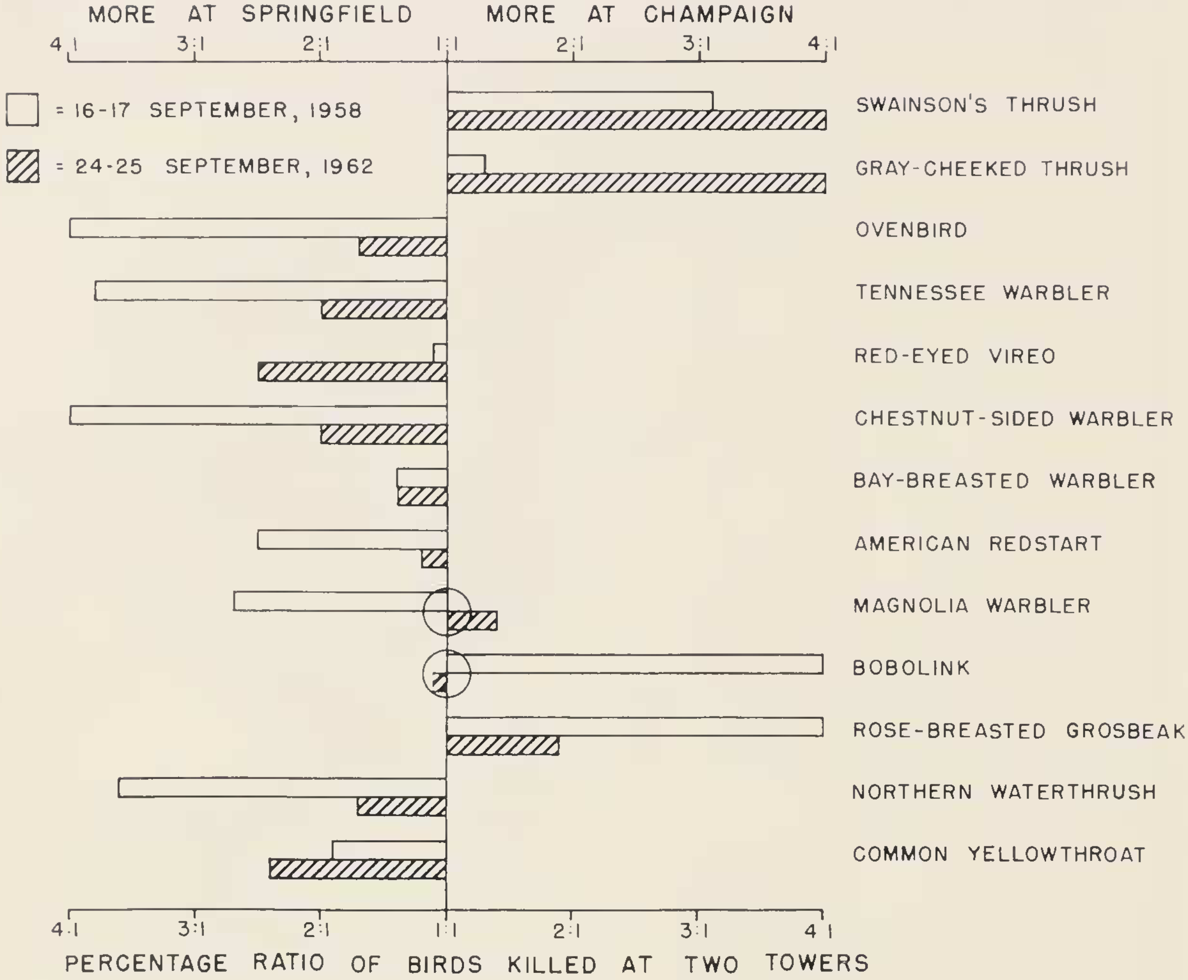

FIG. 17. Comparative numbers of birds of the most common species killed on two nights (different years) at two central Illinois television towers. Note that in most cases if the species was more numerous at Champaign in the first kill, it was also more numerous there the second kill (exceptions encircled).

altitudes above the effective range of the audio system. The behavior pattern that seems best to explain this apparent paradox is that migrants must continue their flight until daylight, but reduce their flight altitude to 1,500 feet or less after midnight, and increase their rate of calling as dawn approaches. Because of the inherent "blindness" of the radar at short range, large numbers of migrants pass at low altitude without being detected. This is clearly shown on nights when migrants are killed at the Champaign tower (981 feet high), though Champaign radar shows no migrants below 1,500 feet. Mascher et al. (1962:215) also concluded that radar missed the low altitude migration in Sweden.

Changes in the rate of calling by migrants tend to coincide with changes in the tracking ratio of the migrant swarm (Fig. 3). The tracking ratio, in turn, reflects either a directional or an altitudinal shift by the migrants.

Thus, both the increased calling rate of migrants after midnight, and the declining numbers of bird targets seen on radar after midnight (Fig. 2) are probably measures of the same phenomenon, i.e., the descending of migrants to lower altitudes.

Though the available data from all points of view seem clearly to indicate that the migrant swarm reduces its altitude after midnight, the shift itself seems inexplicable. It could be interpreted as an intention to land, but there are no data to show that migrants land at night. In populations of long-distance migrants which regularly cross large stretches of open water such as the Gulf of Mexico or the Great Lakes, any tendency to land in the dark would seem to be a liability. The post-midnight altitudinal shift coincides with a directional shift (Fig. 10). The significance of both remains to be discovered.

Why would birds increase their rate of calling after reducing altitude? Calling by migrants increases under an overcast (Fig. 3) and when the birds are changing altitude and/or direction, indicating that the phenomenon is related in some way to orientation or perhaps disorientation of the birds. Hamilton (1962) hypothesized that the night calls of migrants serve to maintain flocks and to convey flight direction information from one member of the flock to another. This hypothesis fits the observation that increased calling coincides with the post-midnight directional shift. It could also be argued that the calls function in spacing or spreading the migrants as an anti-collision system. High calling rate is often sustained following the midnight altitudinal shift even on clear nights, which supports the view that calling is related to spacing, for the reduction in altitude must compress the migrant swarm and increase the flight density. From flight call counts made in the vicinity of a television tower, Cochran and Graber (1958) concluded that migrants were attracted to the structure and its lights. This attraction may exist, but it is now clear that calling rate is an unreliable index to flight density, and that the high calling rate near the tower, like that occurring with overcast skies, reflects a situation of potential peril for the migrants and not necessarily a high flight density. The night calling behavior so prominent among *Hylocichla* thrushes is also well developed in certain Old World species of *Turdus* (Siivonen, 1936), and Vleugel (1951:19) incidentally recorded an instance of increased calling among disoriented thrushes "attracted" to the lights of a city in the Netherlands. The recording of call notes is valuable to indicate the presence of various species of unseen migrants, but as a quantitative record such data may be greatly misleading without some behavioral interpretation.

Estimates of flight densities of migrants have been made on the basis of various techniques of study, including lunar observations (Lowery, 1951), tower kills (Tordoff and Mengel. 1956). and audio and radar studies (Graber and Cochran. 1960; Graber and Hassler. 1962). Data from three of these sources (tower kill. audio and radar) are available for the night of 19–20 September 1960 at Champaign. Flight density estimates from these sources are widely divergent (radar: 70 bird echoes per hour crossing a mile of terrain; audio: 1.300 calls per hour; tower kill: 93.000 birds per hour). Disparity in the estimates is not surprising. Radar misses that part of the migration which occurs at altitudes under 1.500 feet. while the calling rate is exceptionally high on kill nights. The number of calls recorded is almost invariably greater than the number of bird targets detected by radar (Fig. 4). Though the radar is capable of detecting individual birds (Graber and Hassler. 1962). each echo could represent more than one migrant, depending upon their spatial arrangement. The extremely high estimate of flight density from tower kill data is probably a gross distortion because it is based on the assumption that the tower merely cuts a slice out of a uniform migrant swarm as the birds pass. This assumption does not take into account the actual manner in which the kills occur. Migrants approaching the tower enter a lighted area from which they are reluctant to leave. Lovie Whitaker (pers. comm.) pointed out to me that the situation could be compared to that of free-flying birds in a lighted room at night. Even if the doors and windows are open, the birds will not leave the lighted area to fly out into the dark. This is precisely the behavior I have observed at the Champaign tower. On the night of a kill. migrants often fly right through the tower framework and on out toward the edge of the lighted "room" around the tower. only to turn back again toward the light. Circling in this fashion some of them will inevitably strike the dark guys which support the tower.

The kills probably do provide an accurate picture of the night migrant fauna for the place and time they occur. Species commonly killed are also observed commonly in the field (Fig. 5). and for species of comparable conspicuousness. there is significant correlation between the numbers of birds killed and the numbers seen in the field. The tower kill data thus provide at least a tentative base on which to interpret the directional patterns of migration observed by radar.

Despite the gross differences in measurements of the *volume* of migration from different techniques. the audio system. radar. the tower kills all detect the same night-to-night periodicity or *timing* of migration in this area. Consequently we have drawn essentially the same conclusions about the influence of weather on migration from different methods of observation (Graber and Cochran. 1960:254; Hassler. et al.. 1963). Earlier Bennett (1952) perceived the same weather-migration relationships from daily field censuses in Chicago. Apparently many populations of night migrants respond to weather factors in much the same way. Mass flights in September characteristically follow closely a wind shift to northerly, usually to northwesterly, with the passage of a cold front. In fact, the close association of the birds with the front leads to the kill (Graber and Cochran, 1960). The mobile radar shows that the phenomenon is occurring over a broad front and that the directional pattern of the migration is essentially the same along the front across central Illinois. Even the major river valleys, the Mississippi and Illinois, have no obvious effect on the pattern. Night-to-night variation in flight directions of migrants definitely exceeds variation related to locality (Table 3). When the flight directions shift conspicuously, they shift on a broad front (Figs. 11–13). Such marked shifts in flight direction are probably related primarily to changes in the species composition of the migrant swarm rather than to wind shifts or other physical changes. While there may be subtle or even significant variations in the flight directions of migrants from night to night, and even from hour to hour particularly after midnight, and from place to place in central Illinois (Table 3), the consistent east of north pattern in spring and east of south pattern in fall is a dominant characteristic of the migration in this region. Considering the many potential sources of variation in the flight directions, the similarities of the pattern at different times and places are more impressive than the differences (Figs. 6–9; Table 3).

Why is the fall migration direction southeast? Apropos of the constancy of the fall directional pattern is the consistent nature of the species composition of kills at television towers from year to year and place to place in the north-central states (Table 1; Kemper et. al., 1964). The winter ranges of most of these species lie well east of the Champaign meridian (Fig. 8), and the predominantly westerly winds of this latitude tend to carry any air-borne object eastward. In fact the general direction of fall migration, following as it does in the wake of cold fronts, is downwind. Also, based on the geography of the breeding ranges of tower-kill species, more (about 60 per cent) of the population of September migrants nests west of the Champaign meridian than east of it, and the breeding ranges of virtually all of the species extend west of Champaign. Many of the species involved in the September flights are probably of (south) eastern origin (see Mengel, 1961, on the Parulidae).

Lincoln (1950:56) suggested that Bobolinks, in the course of their migration, adhere to ancestral flyways, western populations moving eastward in fall rather than directly toward the wintering grounds. The same pattern of fall migration may be seen in the western race of the Palm Warbler. The migration route of this population is somewhat triangular or perhaps elliptical. In fall much of the population moves eastward (not directly southeast toward the winter range), approaching the Appalachians before turning south toward the South Carolina coast and the Florida Peninsula. That this route greatly concentrates the population during migration is shown by the magnitude of the fall tower kills of western Palm Warblers in northern Florida (Table 2; Stoddard, 1962:75). Like the Bobolink, northeastern populations of the Palm Warbler (the eastern race) move south and southeast down the Atlantic coast in their Fall migration. This flight direction is still downwind, for in fall the postfrontal winds along the Alleghenies are predominantly northeasterly. Do the western populations of these species intentionally move toward the ancestral range, or is the fall flight direction merely a consequence of the temperate zone westerly circulation? To pursue the question further it is worthwhile to examine the migration route of a species such as the Nashville Warbler, which is probably of western origin (see Mengel, 1964:25). In fall, the race of the Nashville Warbler must move southwest, for it is rare in the southeastern U. S., becoming increasingly common along the direct line route between the breeding grounds (eastern Canada and northeastern U. S.) and northern Mexico. Though relatively uncommon at Champaign in fall, Nashville Warblers (eastern race) are occasionally victims of the Champaign tower. They are much more common victims to the north in Wisconsin, and even more common in Minnesota (Kemper et al., 1964:166) and in northeastern Kansas (Tordoff and Mengel, 1956:9). The association of Nashville Warblers (eastern race) with east-oriented species in tower-kill samples shows that Nashvilles migrate behind frontal systems, as the *east*-oriented migrants do. The magnitude of Nashville Warbler mortality at the different towers also indicates that this population does not travel to its wintering grounds (central and southern Mexico) by the most direct route, but stays north of the direct-line route, as western Palm Warblers do on their east-oriented flights. To accomplish their west and southwest migration, Nashville Warblers must compensate for displacement from the northwesterly winds to a much greater extent than do east-oriented populations, which fly more nearly downwind. Thus, a Nashville Warbler going from the center of the breeding range to the center of the winter range would fly a heading aimed well north of the winter range toward Arizona, the center of distribution for this particular complex of *Vermivora* warblers (Mengel, 1964:25). The migration routes of the Nashville Warbler are roughly a mirror image of the Palm Warbler's routes. Just as the *eastern* race of the Palm Warbler has only to fly southward or southwestward to reach its winter range, the *western* race of the Nashville Warbler also has a simpler route (south or southeast) than its eastern counterpart. In both species, the migration routes of the ancestral populations are little affected by the primary westerly circulation.

For east-oriented fall migrants it could be argued that east-orientation has survival value through conservation of energy from "riding the wind" and that the flight direction is unrelated to the ancestral range, but the migration of the Nashville Warbler shows that some populations at least migrate toward the ancestral range in spite of the winds, and at an energy *cost*: the survival value in such a migration is not apparent. The example also suggests that postfrontal "pressure pattern" migration may have some significance to migrants other than that related to energy conservation. The feature of the air mass which would appear to have greatest value to a bird attempting to duplicate the same flight year after year would be constancy (dependability). The more variable the movements of the air, the less favorable would be the bird's chances of duplicating its route. This factor of constancy characterizes the air mass behind the fall cold fronts, and whether or not the airflow is favorable (as it is for east-oriented migrants), it provides a fairly constant and dependable set of conditions in which to migrate. Furthermore, the primary seasonal patterns of the general circulation of the earth's atmosphere have probably not changed significantly in North America since the beginning of the Pleistocene though the temperate zone westerlies may have expanded and intensified during periods of glacial maxima (Willet, 1953:51–54). By responding to the frontal cues migrants can hold a given heading and arrive on the wintering grounds even though the winds are not helpful in reducing the flight time. We might conclude from the example of the Nashville Warbler's migration, that migration routes evolve from the accidental resultant of (1) the bird's heading toward its ancestral range, and (2) the force exerted upon it from the primary patterns of atmospheric circulation over the route. The overwhelming majority of migrants which pass Champaign in fall are east-oriented and *do* benefit from favorable winds. They are probably also mainly of (south) eastern origin.

Clearly, the radar record indicates that the populations of migrants which pass Champaign in spring are different from those which pass in fall. Fall migrants are coming largely from the northwest; the spring birds are moving to the northeast. On the surface, these directional patterns seem to conflict with the accumulating evidence that a given passerine migrant abides in or near the same nesting territory (Nice, 1937:73; Graber, 1961:322) and the same winter "territory" (Robertson, 1961:123; Schwartz, 1963; Nickell, 1962:54; Mewaldt, 1964) year after year, but there is no information on how consistently a migrant retraces its path between its summer and winter home. Mewaldt's (1964) study of displaced White-crowned Sparrows shows that some migrants, at least, need not follow a particular migration route to reach their prescribed destination. In view of this precision in homing, the disparity in the spring and fall flight directions at Champaign seem to indicate that most of the night migrants detected by radar have an elliptical migration route.

For east-oriented trans-Gulf or Antillean migrants, an elliptical migration route fits the general pattern of atmospheric circulation and the positive response of migrants to favorable wind cues both in spring and fall (Graber and Cochran, 1960; Hassler et. al., 1963). Whereas the postfrontal airflow in fall at latitude 40 degrees N is predominantly northwesterly, and in spring, southerly (with a warm front or on the back edge of a high pressure area), winds over the Gulf of Mexico are consistently easterly or southeasterly, except immediately in the wake of cold front passage, when spring migration is halted. Thus, a migrant flying downwind (southeastward) from Champaign in fall, would be moved back westward over the Gulf on its northward passage. Most of the species of long-distance migrants which pass Champaign are trans-Gulf migrants in spring (see Stevenson, 1957). At times the easterly circulation over the Gulf brings large numbers of migrants to the south Texas coast. These flights become especially evident when they meet adverse flying conditions near the coast, as in the dramatic example of a kill reported by James (1956). Most of the 39 species represented in this large kill (2,421 specimens examined) at Padre Island on 6–7 May 1951 are common mid- and late-May migrants at Champaign. Included were 165 Bay-breasted Warblers, 64 Chestnut-sided Warblers, 16 Acadian Flycatchers, 6 Cerulean Warblers, and 4 Golden-winged Warblers. At Padre Island these species were far west of their winter ranges, and near the extreme western meridian of their breeding ranges. Furthermore, the breeding ranges of virtually *all* of the species killed lie mainly (north) east of Texas, so to reach their nesting areas, many of them would almost certainly have had to fly east of north. At the latitude of Texas they were leaving the influence of the easterly winds. At higher latitudes deviations from the south flow become increasingly westerly again, thus completing the elliptical circuit. The bulk of the transients which pass Champaign in May must pass well east of Champaign on their fall flight, while the September migrants must, on their northward flight, pass west of the station.

Field observations at Champaign also tend to support the concept of an elliptical migration, for some populations of transients show marked disparity in the numbers passing between spring and fall: examples are: the Veery (2 in spring to 1 in fall), Solitary Vireo (2 to 1), Blue-winged Warbler (10 + to 1), Nashville Warbler (4 to 1), Parula Warbler (12 to 1), Magnolia Warbler (1 to 12), Cape May Warbler (7 to 1), and Palm Warbler (30 + to 1). The most classic example is the Golden Plover, of which hundreds are seen in spring for every fall record. Much the same trends have been reported for the same species in southeastern Michigan (Kelley et al., 1963).

yet if the same populations passed these areas in both spring and fall, the spring populations would probably be lower, reflecting winter's attrition. Marked differences in the spring-fall ratios for a given species probably reflect primarily a change in the migration route between spring and fall.

The elliptical migration route seems to apply to west-oriented as well as to east-oriented populations. The spring migration of the Palm Warbler fits the general pattern for east-oriented populations, since much of its population comes under the influence of the low latitude easterlies on the northward flight. This westward displacement would definitely bring many more Palm Warblers to Champaign in spring (vs. fall), as our field observations show. But why do more Nashville Warblers pass Champaign in spring than in fall? Such a difference would result only if the Nashville's spring route passed well east of the fall route, reversing the pattern for east-oriented species.

Nashville Warblers, which winter in Mexico, do not come much under the influence of the easterlies: but migrate northward with southerly or southwesterly winds. Given these wind conditions, the Nashville's spring migration route would be east of the fall route if the birds merely reversed their heading from fall to spring. Because most of the long-distance migrants are ultimately of southern origin, we might assume that the spring migration routes would have at least as much zoogeographic significance as the fall routes, if not more. The migration of the Nashville and Palm Warblers does not bear out this supposition. The spring migration of both appears to bear less relationship to the ancestral range than the fall route. It was hypothesized above that the fall migration route evolved from the accidental resultant of the migrant's heading toward its ancestral range and the predominant pattern of postfrontal circulation, and that the complete elliptical migration circuit was greatly influenced by this circulation. It is axiomatic that the spring and fall routes are necessarily interdependent since the end of one is the beginning of the other. The spring route is no less an accident than the fall route, but the relationship of the spring heading to the ancestral range is less apparent because of the displacement which has already occurred in the southward flight. As in the case of the Nashville Warbler, the spring heading for east-oriented populations is probably merely a reversal of the fall heading. The appearance of large numbers of trans-Gulf migrants on the northwest shore of the Gulf (some far west of their winter range and probably west of their destination) is ample evidence of the wind's influence on the migration route, yet by holding a constant southeast heading in fall and reversing that heading in spring a northern migrant will complete an ellipse by timing its flights with the postfrontal circulation. The system is not navigation as observed in species of Old World warblers by Sauer

(1958), but is more like the unidirectional orientation observed in displaced waterfowl by Bellrose (1963) and others. The system could involve various methods of orientation, including the use of celestial (Vleugel, 1954; Sauer, 1958), wind (Vleugel, 1952), and/or even topographic cues. The method which best seems to fit the available data is that the migrants orient on a single point observable over a vast part of the entire route, i.e., most probably celestial orientation. The repeated observation of oriented flight under overcast skies (see Bellrose and Graber, 1963:387) indicates that another effective orientation method may be used by migrants, though at times with poor results (see Fig. 14). The failure, at times, of this auxiliary method of orientation provides a clue to its nature. The system appears to fail when migrants overtake a slow-moving front and pass into an area of variable or calm winds (see Graber and Cochran, 1960:268). Thus, the success of the system seems to depend upon a sustained wind flow: when this condition is lost, the migrants revert to positive phototropic response and orient on any artificial lights near their altitude. This response becomes apparent in the massive kills of birds at TV towers.

Better understanding of the population shifts and migration routes of the many populations passing any locality will come mainly from banding and telemetric studies, but better coverage of more television towers, following the fine example of Stoddard (1962), can greatly augment other types of observations. A comparison of the kills at Champaign with those for the tower in northern Florida studied by Stoddard (1962) during the same span of years (1955–1960) supplements field observations on the migration routes of many species of night migrants. The Florida tower yielded far more specimens, partly because of the superior coverage which Stoddard provided. The average ratio of fall specimens for species killed at both towers was 1 at Champaign to 3.5 in Florida. For some species the numbers of birds killed at the two towers depart greatly from this ratio (Table 2). Aside from the better coverage given the Florida tower, we would expect a greater kill in Florida in view of the southeast directional pattern of migration at Champaign and the fact that most of the species involved are (south) east-oriented in fall. This orientation produces a "funnel effect" (a concentration of the swarm at lower latitudes) along the migration route, which is clearly observable in the kills of some species. Veeries, for example, are killed in a ratio of 52 in Florida to 1 in Illinois. Other species which may show the funnel effect are: the Yellow Warbler, Palm Warbler, Yellow-throated Vireo, Red-eyed Vireo, Northern Waterthrush, Wood Thrush and Yellowthroat (Table 2). A low ratio may indicate either a widely spread migration route for the species or a narrow route which completely misses the Florida tower. It is not surprising that the Florida tower kills only one-tenth as many

Philadelphia Vireos as the Illinois tower, because field observations in general indicate that this species funnels down to the *center* of the Gulf coast so that most of the population passes west of the Florida tower. The low kill of Blackpoll Warblers at the Florida tower supports the view that this species migrates to a large extent off the eastern seaboard (Nisbet et al., 1963), thus east of the Florida tower; the Cape May Warbler may use much the same route (Table 2). The low kills of Scarlet Tanagers, Swainson's and Gray-cheeked thrushes in Florida may indicate that these species pass mainly west of the Florida station over the Gulf; all are uncommon in the Antilles (Table 2).

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